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This volume is dedicated to Dr. Rainer Zangerl

The Brain of *Mesonyx*, A Middle Eocene Mesonychid Condylarth

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INTRODUCTION

The Mesonychidae is a family of medium-sized to gigantic omnivores and carnivores that existed during the Paleocene and Eocene epochs in North America, Europe, and Asia. Mesonychids were formerly classified with creodonts as archaic members of the Order Carnivora (Simpson, 1945, and most earlier workers), but recently have been reassigned to the Order Condylarthra, to better reflect phylogenetic relationships (Van Valen, 1966; Romer, 1966). Condylarths were a heterogeneous group of early Tertiary, predominantly small to medium-sized omnivores and herbivores, from which the various ungulate and subungulate orders were derived. For an introduction to the literature on mesonychids, see Szalay and Gould (1966) and Szalay (1969).

Endocranial casts of representatives of most of the families of condylarths have been described. These are of the arctocyonids *Arctocyonides* and *Arctocyon* (Russell and Sigogneau, 1965); periptychid *Periptychus* (Tilney, 1931; Edinger, 1956); hyopsodontid *Hyopsodus* (Gazin, 1968); phenacodontid *Phenacodus* (Tilney, 1931; Simpson, 1933); meniscotheriids *Pleuraspidotherium* (Russell and Sigogneau, 1965) and *Meniscotherium* (Gazin, 1965); and the tillodontid *Tillodon* (Gazin, 1953). Scott (1888) described a partly exposed natural endocast of *Mesonyx* but his few observations, unsupported by figures or measurements, provide no useful information. The endocast of *Mesonyx* described below is important because it provides the first good

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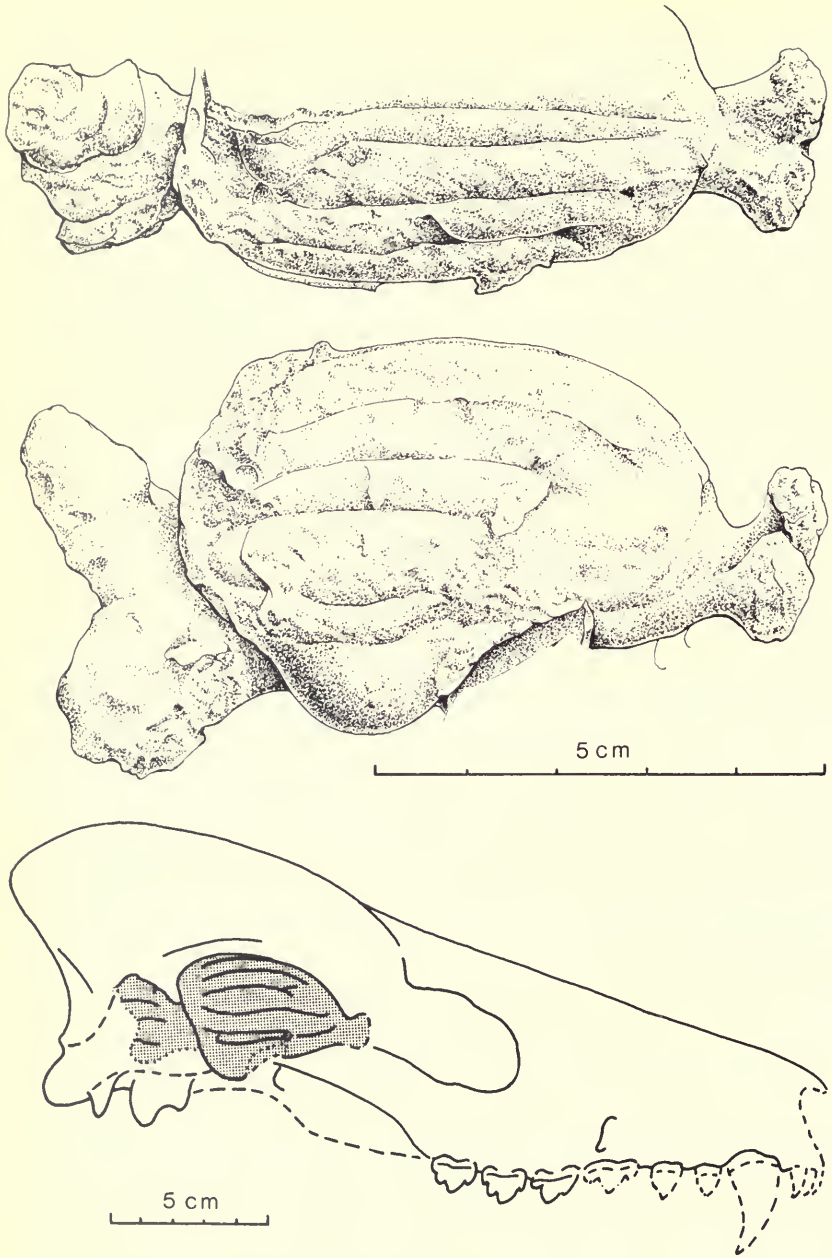


FIG. 1. *Mesonyx obtusidens,* Yale Peabody Mus. 13141. Above, dorsal and lateral views of endocast, approximately natural size. Below, lateral view of endocast in position in skull, approximately x 2/5. Dashed lines indicate estimated boundaries of missing portions; dotted lines indicate border of unexposed portions of endocast.

record of a mesonychid brain, and because it is one of the largest and one of the latest condylarth endocasts known.

DESCRIPTION

A natural endocast was exposed by removing most of the right side of the braincase of Yale Peabody Mus. 13141, a well-preserved, uncrushed skull of *Mesonyx obtusidens,* from the Middle Eocene (Bridger B, about 50 million years old), of Wyoming. The exposed portion of the endocast (fig. 1) includes most of the cerebellum, cerebrum, and olfactory bulbs.

The rhinal fissure is located about two-thirds of the way down the cerebrum, as seen in lateral view. It is well-marked caudally, but rostrally is faint. A cast of a vascular sinus overlies its middle portion, a condition commonly seen in other mammals. Three longitudinally oriented sulci divide the neocortex above the rhinal fissure. The most lateral of these sulci is unusually long and straight compared to what is seen in other mammals, extending for most of the length of the hemisphere. The middle sulcus is shorter, with a faint suggestion of a bifurcation at its rostral end. The medial sulci is almost as long as the bottom one, and it appears to curve slightly laterally at its rostral end.

Enough is preserved of the olfactory chamber to indicate that the olfactory bulbs were slightly pedunculate and relatively small. The pyriform lobe also appears to have been relatively small compared to the rest of the brain (see fig. 2 for comparison with early mammals).

The midbrain was not completely overlapped, for there is a gap of about 5 mm. between the caudal end of the cerebrum and the cerebellar vermis. No details of midbrain morphology are preserved in that space. The vermis is clearly demarcated from the lateral hemispheres, but otherwise little surface detail of cerebellar morphology is evident. The vermis is relatively high and short, with a transverse groove located relatively rostrally. That groove may represent the *fissura prima,* for on most mammal endocasts the *f. prima* is the most prominent, and often the only cerebellar fissure reproduced. There is a faint indication of a longitudinally oriented goove on the side of the cerebellar hemisphere; it may represent the boundary between the ansiform lobule and the paraflocculus. The cerebellar hemispheres extend out about as far laterally as the cerebral hemispheres.

From water displacement of a cast of the *Mesonyx* endocast, with olfactory bulbs and the covered portion of the hind brain restored, I estimate the endocranial volume to have been about 80 cc.

I have exposed the cerebrum of the *Mesonyx* endocast described by Scott (1888), Princeton Univ. 10308. It is somewhat crushed and incomplete, but appears similar in observable details to the Yale specimen. I see no basis for Scott's description of the cerebral hemispheres as very small and the cerebellum as relatively large.

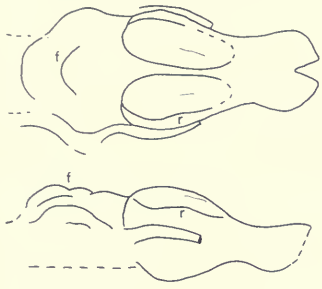
MORPHOLOGICAL COMPARISONS

Factors to consider in comparisons with brains of other mammals are body size, phylogenetic relationship, temporal relationship (geological age), and ecological niche. Most closely related phylogentically to *Mesonyx* are representatives of the other condylarth families. Of these, *Arctocyonides, Hyopsodus, Pleuraspidotherium,* and *Meniscotherium* were considerably smaller than *Mesonyx.* Therefore, the fact that their cerebral hemispheres lacked convolutions or at most had a single neocortical sulcus (see references cited above) does not necessarily indicate a less advanced stage of cortical evolution than in *Mesonyx,* since degree of cortical folding in some groups of mammals appears to be at least in part correlated with absolute brain size, which, in turn, is correlated with body size. The influence of size on degree of gyrencephaly can be seen in series of brains of living prosimian primates (Radinsky, 1974) and ceboid primates (Hershkovitz, 1970). However, such influence does not appear as evident in cercopithecid primates (Connolly, 1950; Radinsky, *pers. observation*) or in canid carnivorans (Radinsky, 1973).

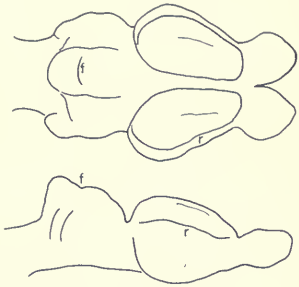
Of the remaining condylarths for which endocasts are known, *Periptychus, Arctocyon, Phenacodus,* and *Tillodon* were closer in body size to *Mesonyx,* although somewhat smaller. The endocast of *Tillodon* is crushed and does not preserve enough surface detail for significant comparison with the other genera. The brain of *Periptychus,* from the Middle Paleocene (about 65 million years old), is known from the dorsal half of an endocast of the fore brain. It has a very high rhinal fissure, and only two small caps of neocortex on top of the cerebrum. The brain of *Arctocyon* (fig. 2A), from

Opposite:

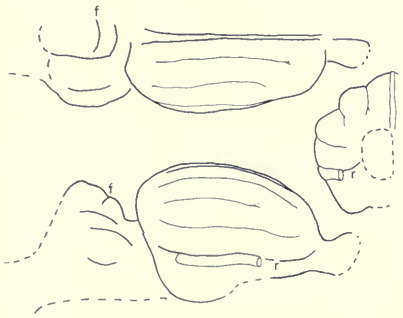
FIG. 2. Drawings of endocasts of condylarths (A, B and C), an early ungulate (D), and early carnivorans (E and F), in dorsal, lateral, and rostral views. See text for discussion. Dashed lines indicate estimated boundaries of missing portions. **A**, *Arctocyon primaevus,* redrawn from Russell and Sigogneau, 1965; **B**, *Phenacodus primaevus,* redrawn from Simpson, 1933; **C**, *Mesonyx obtusidens,* Yale Peabody Mus. 13141; **D**, *Hyrachyus modestus,* Amer. Mus. Nat. Hist. 11713, with cerebellum restored from other specimens; **E**, *Hyaenodon horridus,* Amer. Mus. Nat. Hist. 94760; **F**, *Humbertia angustidens,* Mus. Nat. Hist. Nat., Paris, from a cast of the original specimen. Abbreviations: f, *fissura prima;* r, rhinal fissure. All drawings to same scale, about x 1/2.



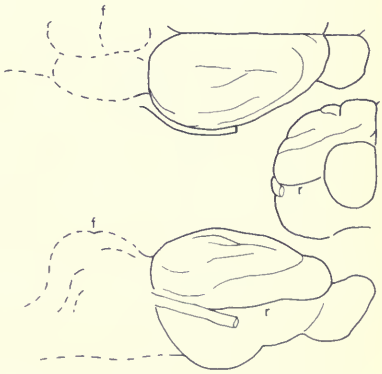
A. *Arctocyon*



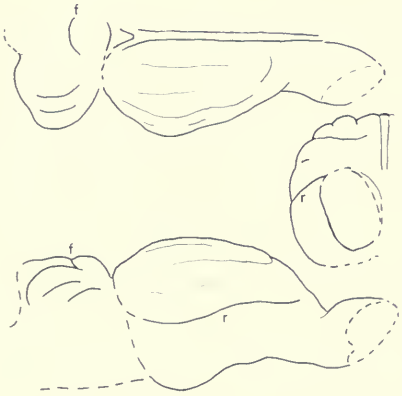
B. *Phenacodus*



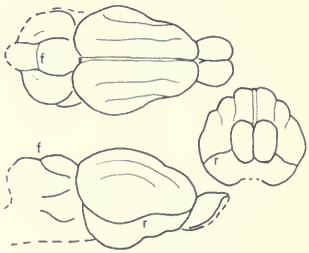
C. *Mesonyx*



D. *Hyrachyus*



E. *Hyaenodon*



F. *Humbertia*

30mm

the Late Paleocene (about 60 million years old), was advanced over that of *Periptychus* in having relatively more neocortex, evidenced by a slightly lower rhinal fissure and the presence of one or possibly two neocortical sulci (surface details are poorly defined on the two known *Arctocyon* endocasts). The midbrain was widely exposed in *Arctocyon.* The brain of *Phenacodus* (fig. 2B), from the Early Eocene (about 55 million years old), was further advanced in having a lower rhinal fissure, with the neocortex covering more of the midbrain and olfactory peduncles than in *Arctocyon.* One or possibly two neocortical sulci were present in *Phenacodus.* (As in the cast of *Arctocyon,* surface details are poorly preserved on the one described endocast of *Phenacodus.)*

The brain of *Mesonyx* was advanced over those of the above mentioned condylarths in having a relatively more expanded neocortex. This is indicated by the relatively more ventrolateral position of the rhinal fissure, the presence of three well-defined neocortical sulci, and the expansion of the cerebrum above the height of the cerebellum. In addition, if the transverse groove on the cerebellar vermis represents the *fissura prima,* it is in a more rostral position than in the other condylarth endocasts, indicating expansion of the neocerebellar portion of the vermis, a progressive trend presumably correlated with the expansion of the neocortex of the cerebrum. The olfactory bulbs are relatively smaller in *Mesonyx* than in the other condylarths in which their size is known. Finally, even allowing for the more ventrally located rhinal fissure, the pyriform lobe appears to have been relatively smaller in *Mesonyx* than in the other condylarths.

There are no other condylarth endocasts of the same geological age or younger than the *Mesonyx* endocast with which it may be compared. The next most closely related group for which Middle Eocene endocasts are known is the ungulate order Perissodactyla, which evolved from phenacodontid condylarths in the Middle or Late Paleocene. *Hyrachyus,* a helaletid tapiroid, was comparable in size to and contemporaneous with *Mesonyx* and therefore suitable for comparison of external brain morphology. The brain of *Hyrachyus* (fig. 2D) appears to have been similar in overall proportions and degree of neocortical expansion to those of other Middle Eocene perissodactyls. Although the rhinal fissure was not as ventrally located in *Hyrachyus* as in *Mesonyx,* its brain also had three well developed neocortical sulci and a fourth short one. However, the rostral end of the most lateral sulcus curved medially and delimited a portion of frontal cortex in *Hyrachyus* that is not so bounded in *Mesonyx.* The brain of *Hyrachyus* further differed from that of *Mesonyx* in having less reduced olfactory bulbs and pyriform lobe, a more caudally located *fissura prima,* and in being narrower across the cerebellum than across the cerebrum. Thus in degree of neocortical expan-

sion, brains of *Mesonyx* and *Hyrachyus* appear to have been similar, although there are differences in details (e.g., lower rhinal fissure in *Mesonyx* and more differentiated frontal pole in *Hyrachyus).* The more rostrally located *fissura prima* suggests that the cerebellum of *Mesonyx* was more advanced than that of *Hyrachyus.* The relatively smaller olfactory bulbs and pyriform lobe of *Mesonyx* are also specialized features.

While mesonychids are phylogenetically closer to condylarths and ungulates than to carnivorans, in general habitus they appear to have been more similar to the latter, particularly during Eocene times (see Szalay and Gould, 1966). Therefore, it is of interest to compare the *Mesonyx* endocast with those of early carnivorans. Archaic carnivorans, called creodonts, unrelated to the ancestry of modern carnivorans, were abundant during the Eocene. However, the earliest known creodont endocasts from animals close in size to *Mesonyx* are from the Oligocene, about 15 million years later in time. The brain of *Hyaenodon horridus* (fig. 2E), a hyaenodontid creodont, was more advanced than the other known Eocene and Oligocene creodont brains. It had two major neocortical sulci, and two shorter, variably developed ones. The lower major sulcus curved medially at its rostral end, as in the Eocene perissodactyls and unlike the straight lower sulcus in *Mesonyx.* However, despite the expansion of the neocortex indicated by the presence of so many sulci, the rhinal fissure in *Hyaenodon* was not as ventrally displaced as in *Mesonyx.* Also, the olfactory bulbs and pyriform lobe are relatively larger and the cerebellar *fissura prima* apparently less rostrally displaced in *Hyaenodon* than in *Mesonyx.*

The modern families of carnivorans, or neocarnivorans, appear to have arisen from a late Eocene adaptive radiation of miacid carnivorans. Judging from the various known Oligocene neocarnivoran endocasts (see Piveteau, 1951; Radinsky, 1971, 1973),the basal neocarnivoran brain was probably similar to that of *Humbertia angustidens* (described under the name *Viverravus* by Piveteau, 1962), a late Eocene miacid. The brain of *Humbertia* (fig. 2F) resembled that of *Mesonyx* in the position of the rhinal fissure, but differed in having only two neocortical sulci (the coronolateral and suprasylvian sulci), with a wide unfolded area of cortex between the lower sulcus and the rhinal fissure. Unlike the conditions in *Mesonyx,* the sulci in *Humbertia* are gently arched; in later carnivorans, the arching becomes even more pronounced. Olfactory bulbs were relatively larger in *Humbertia* and the *fissura prima* less rostrally displaced than in *Mesonyx.* Because of the difference in overall brain size, it is difficult to estimate the relative size of the pyriform lobe in *Humbertia* compared to *Mesonyx.* The midbrain is completely covered by the cerebrum in *Humbertia.*

Because *Humbertia* was considerably smaller than *Mesonyx,* it would be of interest to determine to what degree allometry was responsible for the observed differences in brain morphology, particularly in the number of neocortical sulci. Oligocene neocarnivorans that were closer in size to *Mesonyx,* such as the amphicyonids *Amphicyon* and *Daphoenus,* and the canid *Mesocyon,* had brains that were similar in most features to that of *Humbertia,* but had in addition a third sulcal arch, the ectosylvian sulcus, beneath a more convex suprasylvian sulcus (Beaumont, 1964; Radinsky, 1971, 1973). Small early neocarnivorans generally lack an ectosylvian sulcus, which suggests that its absence in the Late Eocene *Humbertia* might be due to allometry. In addition to the ectosylvian sulcus, some but not all large early neocarnivorans have one or two short secondary sulci, the ectolateral and entolateral sulci, adjacent to the caudal end of the cornolateral sulcus.

RELATIVE BRAIN SIZE

Most of the statements in the literature on relative brain size of fossil mammals are unsupported assertions that brains were relatively small in any given extinct species. For example, Scott (1888, p. 155) wrote that *Mesonyx* had an exceedingly small brain capacity, but did not specify his point of comparison, and gave no measurements of endocranial capacity. However, during the past 10 years, Jerison (1973 and references cited therein) has provided a large body of quantitative data on relative brain size in fossil mammals, based on endocranial volumes (used interchangeably with brain weights) and body weights (estimated from various skeletal measurements). For purposes of comparison, Jerison uses an Encephalization Quotient, or EQ, which is defined as the endocranial volume (or brain weight) of a given species divided by the endocranial volume one would expect to find in an "average" living mammal of that species' body weight. The relationship between brain weight and body weight in Jerison's "average" living mammal is described by the equation, $E = 0.12\ P^{0.67}$, (E = brain weight; P = body weight), based on a large sample of living mammals. Bauchot and Stephan (1966) compare relative brain sizes of recent mammals in a similar manner, except their Encephalization Index is based on a comparison with the brain size one would expect in a basal insectivore of a given body weight. For brain weight-body weight comparisons, I would have preferred to use Bauchot and Stephan's basal insectivore line as a standard, since the equation describing relative brain size in basal insectivores is unlikely to change with the addition of more data, while the equation for the "average" living mammal is more likely to vary depending on what species are included in the sample. However, since Jerison has calculated EQs for a large number of fossil

Table 1. Relative brain size in Condylarths.

Species	Endocranial volume (cc.)	Skull length (SL, cm.)	Estimated Body length (cm.)	Estimated Body weight (gms.)	Encephalization Quotient (EQ)[1]	EQA[2]
Mesonyx obtusidens YPM 13141	80	26	117(4.5SL) to 130 (5SL)	40,040 to 54,900	0.57-0.46	1.13
Arctocyonides arenae MNHN CR733	12	12	60 (5SL)	5,400	0.32	0.87
Arctocyon primaevus MNHN CR700	37	23.5	106 (4.5SL) to 118 (5SL)	29,565 to 40,556	0.32-0.26	
Meniscotherium robustum USNM 19509	12	13	65 (5SL)	6,866	0.27	0.77
Phenacodus primaevus AMNH 4367	35	23.7	130 (measured)	54,925	0.20	0.53

[1] EQ is the brain size of a given species divided by the brain size expected for an "average" living mammal of that species' body weight. See text for further information.

[2] Encephalization quotient based on comparison with foramen magnum area rather than body weight. See text for further information.

mammals, to facilitate comparisons with his data I have used EQ to provide a quantitative measure of relative brain size in *Mesonyx.*

Data for estimations of relative brain size in *Mesonyx* and other condylarths for which such data are available are presented in Table 1. Endocranial volumes were measured by water displacement of endocasts, (or copies of endocasts), with distorted or missing parts restored. My estimate of endocranial volume *Arctocyonides* differs from that of Jerison (1973, Table 11.1). Body weight was estimated from body length, using the equation $P=.025\ L^3$, which was calculated by Jerison (1973, p. 53) from a large sample of living ungulates and carnivores. For *Arctocyon* and *Arctocyonides,* Jerison used the equation $P = .050\ L^3$ to calculate body weight, which resulted in lower EQs than I calculated, but from the known skeletal remains of those genera I see no reason not to use the same equation as for the other condylarths. Body length (skull and trunk length) could be measured directly only in *Phenacodus;* for the other genera I estimated it from the proportions of skull length to body length in other specimens or in related genera.

The Encephalization Quotient for *Mesonyx obtusidens* is 0.46 or 0.57, depending on the estimate of body length used. EQs for the other condylarths ranged from 0.20 to 0.32, all under the *Mesonyx* minimum estimate. For Middle Eocene perissodactyls, Jerison *(ibid.)* estimated three EQs, ranging from 0.37 - 0.49; for the *Hyrachyus* specimen shown in Figure 2D, I estimated an EQ of 0.36 or 0.52, depending on the body length estimate used. For four Eocene and Oligocene creodont carnivores, Jerison *(ibid.)* calculated EQs ranging from 0.33 - 0.55; for my *Hyaenodon horridus* specimen, I estimate an EQ of 0.61. For a sample of early neocarnivorans, Jerision calculated EQs ranging from 0.32 - 0.79. Thus, compared to contemporaneous perissodactyls and to creodonts and early neocarnivorans, *Mesonyx* did not have a relatively small brain.

For comparison of relative brain size of *Mesonyx* with modern species, I calculated mean EQs and the observed range of EQs for representative samples of living insectivorans (data from Bauchot and Stephan, 1966), of artiodactyls (the dominant surviving ungulates), and of carnivorans (see table 2). Relative brain size of *Mesonyx* was in the upper part of the observed range of relative brain size of living insectivorans, in the lower part of the observed range of living artiodactyls, and around the lower end of the observed range of living carnivorans.

One of the problems with analyzing relative brain size by the above method is the uncertainty involved in estimating body weight of extinct species from skeletal measures. Even where complete skeletons are available, and body length can be measured directly, it is evident from the graph presented by Jerison (1973, p. 53, fig. 2.9) that there is a high degree of

variability in the body length-body weight relationship. Unfortunately, Jerison does not provide calculations of the variance, but it appears from his graph that for a mammal of 100 cm. body length, the observed range of body weight is from 10 kg. to about 35 kg. This problem might be minimized if one could calculate EQs for several related, approximately contemporaneous species, for errors of body weight estimates would probably be random and therefore with a large enough sample would cancel each other out. However, *Mesonyx* is the only mesonychid for which brain size can be estimated, and there are not even any other condylarths of Middle Eocene age available with which it can be compared. Therefore, it is desirable to have another method of estimating relative brain size to provide a check on the Encephalization Quotient calculated for *Mesonyx*.

Plots of brain weight *vs.* foramen magnum area for six groups of living mammals (insectivorans, rodents, prosimian primates, artiodactyls, carnivorans, and monkeys) show approximately the same relative relationships as do brain weight-body weight plots of those groups (Radinsky, 1967). For a sample of 164 recent mammal species of those six groups, the coefficient of correlation (r) between foramen magnum area and body weight is 0.98. Removing the influence of brain weight, the partial correlation of foramen magnum area and body weight is 0.65. Therefore, it seems reasonable to

Table 2. Relative brain size in some living mammals.

	Encephalization Quotients[1]		EQA[2]	
Order	Mean	Observed Range	Mean	Observed Range
Insectivora[3] (N = 24)	0.47	0.24-0.83	0.41	0.20-0.68
Artiodactyla[4] (N = 36)	0.81	0.39-1.29	1.08	0.69-1.52
Carnivora[5] (N = 48)	0.89	0.52-1.80	1.37	0.88-2.62

[1] EQ is the brain size of a given species divided by the brain size expected for an "average" living mammal of that species' body weight. See text for further information.

[2] Encephalization quotient based on comparison with foramen magnum area rather than body weight. See text for further information.

[3] Brain weight and body weight data from Bauchot and Stephan, 1966.

[4] Body weight data from Kruska, 1973, and Walker, 1964.

[5] Body weight data from Walker, 1964.

examine the relationship between brain size and foramen magnum area in *Mesonyx* as a check on the relative brain size as estimated from body weight. To facilitate comparisons, I calculated the equivalent of the EQ for foramen magnum data. The EQA of a given species is the observed brain size of that species divided by the brain size one would expect in an "average" living mammal of that species' foramen magnum area. In my sample of 164 species of insectivorans, rodents, prosimians, artiodactyls, carnivorans, and monkeys, the average brain weight-foramen magnum area relationship is expressed by the equation $E = 22.4\ A^{1.48}$, or $\log E = 1.35 + 1.48 \log A$ (A = foramen magnum area, cm^2). The results of this approach are presented in Tables 1 and 2.

Relative brain size in *Mesonyx* based on the foramen magnum area comparison is higher than that of *Arctocyonides, Meniscotherium,* and *Phenacodus,* the other condylarths for which the relevant data are available, and comparable to that of early perissodactyls and carnivorans (Radinsky, unpublished data). This confirms the analysis based on body weight comparisons. However, compared to the recent species, EQAs of *Mesonyx* and the other condylarths are higher relative to their EQs. Thus on the basis of foramen magnum area, relative brain size in *Mesonyx* is above the observed range of insectivorans, just above the mean for artiodactyls, and well within the lower part of the observed range for carnivorans. Two possibilities to account for this difference are that we have overestimated body weights for the extinct genera (and thus have EQs that are too low), or that the relationship between foramen magnum area and body weight is different in the living species compared to the fossil ones.

CONCLUSIONS

The brain of *Mesonyx* was relatively larger and more advanced in terms of expansion of neocortex (and probably also neocerebellum) than the other known condylarth brains with which it may be compared. The latter, however, are from earlier time periods than *Mesonyx.* The brain of *Mesonyx* was roughly comparable in relative size and in degree of neocortical expansion compared to brains of contemporaneous perissodactyl ungulates and slightly younger (geologically) carnivorans. The cerebellar *fissura prima* appears to be rostrally displaced in *Mesonyx* compared to early ungulates and carnivorans, suggesting a relatively more expanded neocerebellum.

The brain of *Mesonyx* was more specialized than that of other condylarths and of early ungulates and carnivorans, in having relatively small olfactory bulbs and apparently a relatively smaller pyriform lobe. The relative size of the pyriform lobe is difficult to estimate, and its apparent reduc-

tion in *Mesonyx* may in part be an illusion resulting from the relatively great expansion of the neocortex. If the pyriform lobe was indeed relatively small in *Mesonyx,* that may be correlated with the reduction of the olfactory bulbs, since the pyriform lobe cortex is usually considered to be mainly involved in olfactory function.

The rhinal fissure was more ventrally displaced in *Mesonyx* than in the early ungulates and carnivorans that had a similar number of neocortical sulci, suggesting either a greater degree of neocortical expansion in *Mesonyx* or that its sulci were shallower.

The sulcal pattern of *Mesonyx* is so different from that of ungulates and carnivorans (or of any other mammal), that I hesitate to attempt to identify sulci and interpret functional areas of the cortex. The only functional interpretation that is apparent from the known brain morphology of *Mesonyx* is reduction in importance of olfaction, indicated by the apparently reduced olfactory bulbs. I see no features of the brain of *Mesonyx* that suggest phylogenetic affinity to any other group of mammals.

ACKNOWLEDGEMENTS

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